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14. ABSTRACT

Activities of sedimentary infauna have significant consequences on overall sedimentary diagenesis. Infauna directly participate in sedimentary processes by organic matter metabolization coupled to aerobic respiration and metabolite excretion. In addition, they indirectly influence the diagenetic pathways by changing the transport regimes of dissolved and particulate species as well as by modifying microbial habitats. The couplings between infaunal activities and their biogeochemical consequences have been studied in recent years, but many of the results and conclusions remain site- and species-specific due to the diverse and highly interrelated ways in which sedimentary infauna interact with the transport, reaction, and microbial regimes. A generalized understanding of infauna-influenced sedimentary systems will require (1) a systematic classification of the infauna–sediment interaction mechanisms

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8

Biogeochemical Consequences of Infaunal Activities

Yoko Furukawa

Abstract

Activities of sedimentary infauna have significant consequences on overall sedimentary diagenesis. Infauna directly participate in sedimentary processes by organic matter metabolization coupled to aerobic respiration and metabolite excretion. In addition, they indirectly influence the diagenetic pathways by changing the transport regimes of dissolved and particulate species as well as by modifying microbial habitats. The couplings between infaunal activities and their biogeochemical consequences have been studied in recent years, but many of the results and conclusions remain site- and species-specific due to the diverse and highly interrelated ways in which sedimentary infauna interact with the transport, reaction, and microbial regimes. A generalized understanding of infauna-influenced sedimentary systems will require (1) a systematic classification of the infauna–sediment interaction mechanisms and (2) a comprehensive model framework that incorporates all known effects of infauna–sediment interactions associated with transport, reaction, and microbial regimes.

Introduction

Sedimentary infauna affect the course of early diagenesis. Their direct participation in organic carbon (OC) degradation and metabolite production is quantitatively significant. They also modify chemical reaction regimes and microbial habitats by providing sites for intense geochemical and redox oscillation and gradients, as well as by rapidly redistributing OC and other redox-sensitive species. In addition, the sedimentary fabric is modified due to their activities, altering physical transport regimes.

During the 40 years since Berner presented the idealized model for sedimentary early diagenesis [Berner, 1964], many studies have explored ways to describe net infaunal contributions, using mathematical models with one-dimensional (1D; i.e., vertical) reaction and transport geometry. The infaunal redistribution of sediment particles and dissolved species has been represented as a vertical diffusive process using the biodiffusion coefficient [Wheatcroft et al., 1990]. One-dimensional irrigation coefficients have been widely used to represent the vertical redistribution of dissolved species due to infaunal ventilation of their burrow habitats [Emerson et al., 1984]. The net enhancement of microbial OC remineralization rates resulting from this has typically been described with phenomenological first-order rate constants. The 1D model geometry and phenomenological rate expressions have provided a useful framework for researchers to quantitatively evaluate reaction and transport

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rates between different depth horizons and among various sedimentary environments. Comparison between modeled and observed depth profiles of geochemical species can provide insights into and improve our current understanding of early diagenetic systems, for example, whether the system of reactions used in the particular model includes all of the quantitatively significant reactions, or whether the function used to represent irrigation coefficient is adequately portraying the depth dependency.

Recently we have become more aware of the lateral and temporal heterogeneity of sediments, as well as its significant consequences to overall diagenesis. For example, rates and magnitudes of microbial OC degradation were found to be greater in experiments with redox oscillation than in experiments with steady-state redox conditions [Aller, 1994]. Sedimentary particles experience such redox oscillation as they are transported across lateral and horizontal redox boundaries. An in situ experimental study has shown that the effect of redox oscillations on OC degradation is due to the interdependence between aerobic and anaerobic microorganisms [Hulthe et al., 1998]. Redox oscillations encourage the repeated reoxidation of reduced iron phases and formation of poorly crystalline Fe(III) minerals that are more readily utilized as terminal electron acceptors than crystalline Fe(III) minerals [Jensen et al., 2003]. Temporally heterogeneous pulse input of labile OC stimulates the microbial metabolism [Hee et al., 2001]. As a consequence, an increasing number of studies are now focusing on the descriptions of temporally and spatially heterogeneous distributions of individual processes and mechanisms, as well as their interrelationships and net consequences for sediment biogeochemistry, rather than simply averaging the heterogeneity to fit *a priori* model geometries [Gilbert et al., 2003a; Glud et al., 2001; Hulth et al., 2002].

Phenomenological first-order rate constants, although useful in comparative studies, do not readily provide mechanistic descriptions of the interrelated processes. For example, in bioirrigated sediments, the first-order net rate constant for the OC degradation, k_{OC}, in the following equation

$$\frac{dC_{OC}}{dt} = -k_{OC}C_{OC} \tag{1}$$

where C_{OC} is the OC concentration and t is time, is a function of the nature of labile OC compounds as well as of a variety of environmental variables, including concentrations of terminal electron acceptors (TEA) and toxic metabolites, microbial activities, and net solute transport regimes [Aller and Aller, 1998]. The environmental variables listed here are all interrelated. Consequently, the adjustment required for k_{OC} to describe observed rate enhancement due to bioirrigation, for example, is a net result of complex interactions between the variables. It is ultimately desired to mechanistically understand how k_{OC} is independently related to each variable if we are to build general models with few adjustable parameters that can be applied in all sedimentary environments for the quantitative characterization of geochemical fluxes and cycles of nutrients and carbon. In addition, a mechanistic understanding is prerequisite to predicting the consequences of environmental manipulations such as environmental remediation efforts and coastal dredging. The current surge in the study of heterogeneous processes and their interrelationships should expand our mechanistic understanding as well as our ability to build quantitative, mechanistic, and general models.

This chapter will summarize the biogeochemical consequences of sediment–macrofauna interactions with emphasis on the effects of temporal and spatial heterogeneity of infauna activities. It is intended to be a guide for planning the further mechanistic studies of individual processes and their interrelationships and for the further incorporation of such understandings into the model frameworks of sediment early diagenesis.

Infauna-Induced Heterogeneity and Its Effects

Laterally Heterogeneous Solute Transport Geometry due to Burrows

One of the most notable effects of sedimentary infauna on biogeochemical mass transfer is the creation of a complex, three-dimensional reaction and transport geometry. The steep geochemical and redox gradients observed at the water–sediment interface (WSI) of shallow, fine-grained sediments are also present along burrow walls where oxygenated burrow water borders anoxic sediments enriched in metabolites and reduced species. At burrow walls, much like at the WSI, dissolved O_2 concentrations often vary between saturation and complete depletion within few millimetres due to extremely rapid consumption of O_2 by microorganisms as well as by reoxidation of reduced species [Jørgensen and Revsbech, 1985]. The additional interface between oxygenated water and anoxic sediments represented by burrow walls can significantly increase the diffusive uptake of dissolved O_2 by sediments [Furukawa et al., 2000; Wenzhofer and Glud, 2002] [Figure 1]. The additional interface promotes fluxes of many other geochemical species as well.

The geometry of burrows created by infauna depends on the species present, population density, as well as the physiological responses of infauna to environmental factors, all of which are in turn dictated by the climatological, geological and oceanographical characteristics of each particular site [Cutter and Diaz, 2000]. These properties are always site-, season- and species-specific, making generalization attempts difficult. Burrow geometries are complex even in laboratory systems populated by single species of burrowing organisms [Figure 2]. The defining variables for individual burrow geometry such as the radius, vertical extent of the burrows, and tilt angle, as well as the variables describing the assemblage such as the burrow opening density and distribution, take even wider ranges of values in natural sediments populated by multiple species [D'Andrea and Lopez, 1997].

Complex burrow geometries may be represented using simple, positive functions of the burrow surface area per unit volume of sediments, using the original model by Aller [1980]

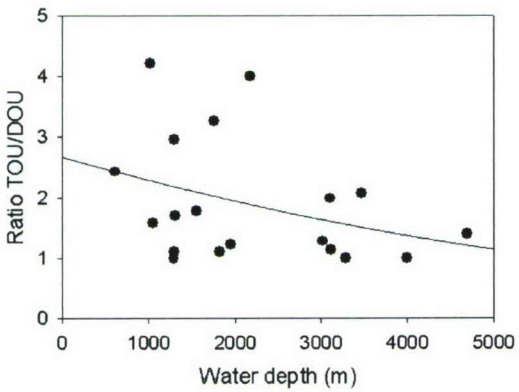

Figure 1. Comparison of diffusive oxygen uptake (DOU; oxygen flux value determined from measured O_2 microprofiles at WSI by assuming all O_2 flux occurs at WSI), and total oxygen uptake (TOU; oxygen flux value directly measured using benthic chambers). Measurements are from the eastern and western South Atlantic. TOU is greater than DOU in shallow water environments, where the activities of benthic macrofauna are significant, whereas the difference becomes negligible in deep water regions, where burrows are sparse. From Wenzhofer and Glud [2002].

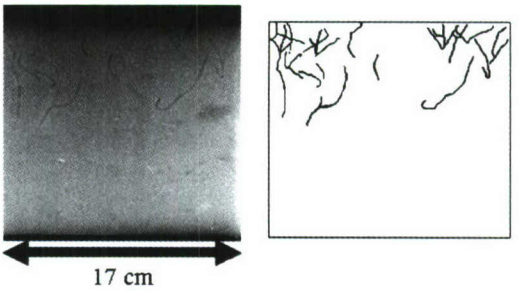

Figure 2. The X-radiograph image of a slab-shaped core (0.17 m × 0.022 m opening × 0.15 m deep) from an estuarine sediment simulated in a laboratory mesocosm populated with a single macrofaunal species (*Schizocardium* sp.) at a population density of 356 individuals m^{-2} [Furukawa et al., 2001]. The binary depiction of *Schizocardium* burrows captured inside the slab core is also shown.

in which burrowed sediments are modeled as laterally close-packed identical vertical cylinders containing tube-shaped voids [Figure 3]. Although the model geometry is highly idealized compared to burrowed sediments in nature, it offers a framework for evaluating processes around burrow walls. In the model, enhanced solute transport due to infaunal burrow ventilation is expressed as the radial diffusive transport perpendicular to the burrow axis. Burrow water composition is assumed to be identical to that of overlying water. Consequently, the concentration of a given solute species at a given spatial position (x,r), $C_{x,r}$, can be determined by a steady-state conservation equation that relates the 2D (vertical, x, and radial, r) solute distribution to vertical diffusion perpendicular to the WSI, radial

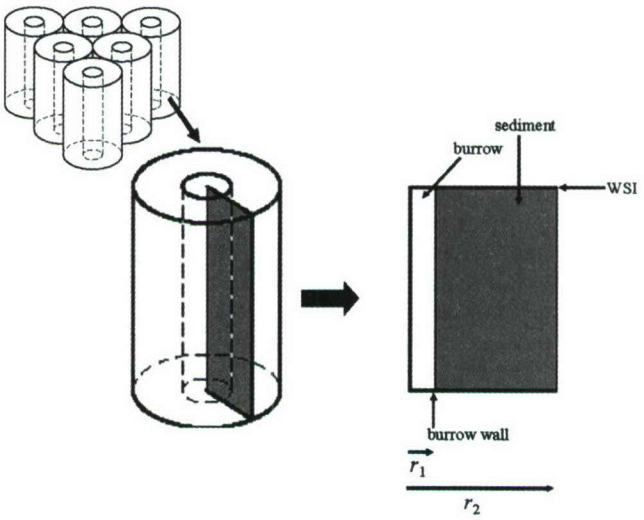

Figure 3. The model geometry for burrowed sediments developed by Aller [1980], with r_1 = burrow radius and r_2 = half-distance between burrows.

diffusion perpendicular to the burrow axis, and net biogeochemical reactions involving the solute:

$$D'\frac{\partial^2 C_{x,r}}{\partial x^2}+\frac{D'}{r}\frac{\partial}{\partial r}\left(r\frac{\partial C_{x,r}}{\partial r}\right)+R=0 \tag{2}$$

where $D' \equiv$ tortuosity-corrected diffusion coefficient of the solute of interest and $R \equiv$ net reaction rate for the production and consumption of solute [Aller, 1980]. For simplicity, in this review sediment accumulation and erosion (i.e., advection) are not considered, and porosity is assumed to be constant. Further, it has been shown that Eq. 2 is related to the following, widely used 1D diffusion-bioirrigation-reaction equation:

$$D'\frac{d^2\overline{C}_x}{dx^2}-\alpha(x)(\overline{C}_x-C_0)+\overline{R}=0 \tag{3}$$

by the irrigation coefficient $\alpha(x)$:

$$\alpha(x)=\frac{2D'r_1}{(r_2^2-r_1^2)(\overline{r}-r_1)} \tag{4}$$

where $C_0 \equiv$ solute concentration in overlying water, $\overline{C}_x \equiv$ radially averaged concentration at depth x, $\overline{R} \equiv$ radially averaged net reaction rate, $r_1 \equiv$ model burrow radius, $r_2 \equiv$ half distance between two model burrows, and $\overline{r} \equiv$ radial distance from the burrow axis to the point where concentration of the solute equals the horizontally averaged concentration value [Boudreau, 1984]. It should be noted, however, that Eq. 2 and Eq. 3 are equivalent only for species whose concentration gradients at the burrow wall are similar to the linear concentration gradients between r_1 and $\overline{r}$. The use of the irrigation coefficient as expressed in Equation (4) may therefore not be appropriate for species that are depleted in the vicinity of burrow walls due to rapid consumption [Berg et al., 2003].

Real burrow geometries are complex as they are not all identically shaped, equally spaced, nor perfectly vertical. Still, the Aller [1980] model framework may be applied to complex burrow geometries by focusing on the burrow surface area per unit volume of sediments. This is because an examination of Eq. 4 above shows that the irrigation coefficient is a positive function of burrow radius, r_1, and the burrow density per unit lateral area, N, both of which are positively related to the burrow surface area. Thus, Koretsky et al. [2002] has shown that $\overline{r}$ can be expressed as a function of r_1 and r_2 using the following equations:

$$\overline{r}=\exp\left(-\frac{f(\gamma)}{2}-\frac{3}{4}+\ln r_2+\frac{1}{2}\left(\frac{r_1}{r_2}\right)^2-\frac{1}{4}\left(\frac{r_1}{r_2}\right)^4\right) \tag{5a}$$

where:

$$f(\gamma)=\gamma-\gamma^2+\frac{3}{2}\gamma^3-\frac{8}{3}\gamma^4+\frac{125}{24}\gamma^5-\frac{154}{5}\gamma^6+\frac{16807}{720}\gamma^7-\frac{16384}{315}\gamma^8+\frac{1531441}{4480}\gamma^9 \tag{5b}$$

$$\gamma = -\frac{1}{r_2^2}\exp\left(-\frac{1}{r_2^4}\left(1.5r_2^4 - 2r_2^4 \ln r_2 - r_1^2 r_2^2 + 0.5r_1^4\right)\right) \tag{5c}$$

while the lateral close-packed geometry of Aller [1980] yields a simple relationship between r_2 and N:

$$r_2 = \sqrt{\frac{1}{2\sqrt{3}N}} \tag{6}$$

Consequently, when Eq. 6 replaces r_2 in both Eq. 4 and Eq. 5, and Eq. 5 replaces $\bar{r}$ in Eq. 4, $\alpha(x)$ can be expressed as a function of r_1 and N as long as the value of D' is known. The resulting expression for $\alpha(x)$ yields Figure 4, which illustrates that $\alpha(x)/2D'$ is a positive, but not necessarily linear, function of r_1 and N.

Several previous studies have attempted to generalize complex burrow geometries using burrow surface areas as the controlling variable. For example, complex burrow geometries directly observed with X-radiography have been idealized using a cone-shaped central void with a radius that decreases with depth to match the depth-dependent decrease in measured burrow wall surface area [Furukawa et al., 2001]. Other studies have used the burrow surface area per unit area of seabed as the single defining parameter to describe complex burrow networks and approximate biologically enhanced solute transport [Bartoli et al., 2000; Davey, 1994].

These generalization approaches, where the complex burrow geometry is represented by depth-dependent description of burrow surface area, are reasonably successful in describing 1D, vertical reaction and transport during early diagenesis. They are also potentially capable of describing micro-scale; heterogeneous processes that occur in the immediate vicinity of

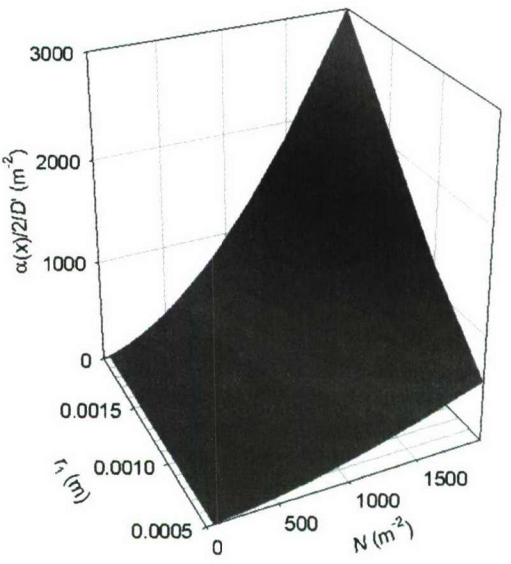

Figure 4. Irrigation coefficient divided by $2D'$ (i.e. $\frac{\alpha(x)}{2D'}$) as a function of both r_1 and N.

burrow walls, such as the extremely rapid consumption of dissolved O_2. However, currently these approaches can only be implemented after a direct observation of burrow geometry by X-radiography, resin cast, sediment profile imagery, or computer-assisted axial tomography [Davey, 1994; Furukawa et al., 2001; Michaud et al., 2003; Rhoads and Germano, 1982].

These observation methods are extremely site-specific and time-consuming. The recently proposed stochastic approach, in which site-specific ecological data (i.e., macrofauna speciation and population density) are combined with the general knowledge of burrowing habits of species present [Koretsky et al., 2002], may become more practical in the near future as ecological data become available for more macrofauna species and more sedimentary environments. In the stochastic model formulation, the irrigation coefficient is expressed as a function of burrow number and radius, as shown in the discussion above. Instead of directly measuring or estimating the values of r_1 and N from observations, however, the model takes advantage of existing literature data that statistically represent the burrow numbers and geometries, which can then be converted to r_1 and N values.

Biogeochemical Dynamics of Burrow Water

While the Aller [1980] approach and other simplified burrow geometries offer a reasonable transport framework for the quantitative description of the geochemical processes occurring at the burrow wall, they need to be supplied with boundary conditions to determine the effect of infauna burrowing on biogeochemical mass transfer. Originally, applications of the Aller [1980] model assumed that the burrows were continuously ventilated with overlying water and thus the solute concentrations inside burrows and at burrow walls were identical to those of the WSI (i.e., $R = 0$ and $C_{x,r,t} = C_0 =$ constant within burrow tubes where C_0 is the concentration of a dissolved species in the overlying water). However, it has since been documented that several commonly found species of burrowing infauna alternate between ventilation and rest periods [e.g., Figure 5] [Forster and Graf, 1995; Kristensen, 1989; Kristensen, 2001; Riisgård, 1991]. Recent innovations in the planer arrays of optodes have visualized the time-dependent fluctuations in the dissolved O_2 concentration of an infaunal burrow presumably associated with the ventilating and resting phases of infaunal activity [Glud et al., 2001]. In addition, direct measurements of NH_4^+ excretion by polychaetes suggest that the burrow water becomes enriched in metabolites such as NH_4^+ and ΣCO_2 during the rest periods when metabolic production of NH_4^+ and ΣCO_2 continues, while no burrow ventilation removes them [Nithart et al., 1999]. Polychaetes occupying laboratory-simulated burrows were also found to enrich their habitats with NH_4^+ during rest periods [Kristensen et al., 1991b].

A non-steady state, time-dependent version of Eq. 2 above, *i.e.*,

$$\frac{\partial C_{x,r,t}}{\partial t} = D' \frac{\partial^2 C_{x,r,t}}{\partial x^2} + \frac{D'}{r} \frac{\partial}{\partial r} \left(r \frac{\partial C_{x,r,t}}{\partial r} \right) + R_{x,r,t} \tag{7}$$

can simulate the geochemistry of sediment surrounding a burrow experiencing alternating ventilation and rest periods as well as the metabolite build-up during the rest periods by (i) setting up appropriate durations for ventilation and rest periods; (ii) forcing $C_{x,r,t} = C_0 =$ constant and $R = 0$ inside the burrow and at the burrow wall for the duration of ventilation periods; and (iii) incorporating the rates of metabolite production by infauna into R inside the burrow for the duration of rest periods [Furukawa, 2001; Marinelli and Boudreau, 1996]. The solution to Eq. 7 for a typical scenario of 54-min *Nereis virens* ventilation cycles (i.e., 40-min rest periods followed by 14-min ventilation periods;

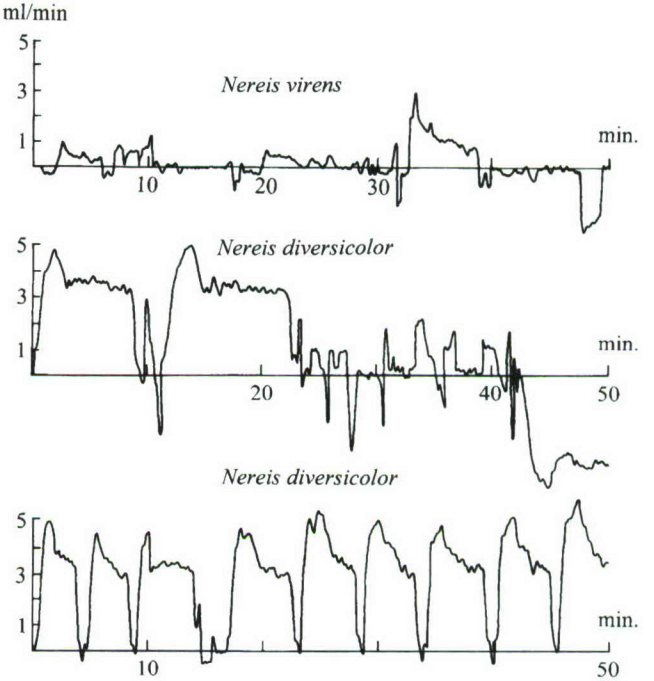

Figure 5. Burrow ventilation patterns observed for *Nereis virens* (top), *N. diversicolor* during a non–suspension-feeding period (middle), and *N. diversicolor* during a suspension-feeding period (bottom) [Kristensen, 1989; Riisgård, 1991], expressed as the time-dependent change in the flow rate of water in the immediate vicinity of burrow openings. The diagram is from Kristensen [2000].

population density of 1,200 m^{-2}; burrow radius of 3×10^{-3} m; and infaunal ΣCO_2 excretion rate of 2×10^{-7} M s^{-1} [Kristensen, 1989]) points to significant oscillations in ΣCO_2 concentrations inside of and adjacent to the burrow [Figure 6]. Similarly significant geochemical oscillations can be seen in other solute species. The O_2 concentration fluctuates between fully aerobic and nearly anoxic inside of and immediately adjacent to the burrow, and the oscillations in ΣCO_2 leads to significant oscillations of pH inside of and immediately adjacent to the burrow [Furukawa, 2001]. Additional assumptions required to solve Eq. 7 include: (i) constant diffusive tortuosity throughout the sediment; and (ii) the coupling of concentrations and reaction rate coefficients of all major biogeochemical species (i.e., O_2, NO_3^-, SO_4^{2-}, NH_4^+, ΣS^{2-}, and ΣCO_2) is determined as previously described in multi-component reaction-transport modeling studies [Boudreau, 1996; Van Cappellen and Wang, 1996]. These calculation results illustrate the significant redox and other chemical oscillations caused by periodic burrow ventilation.

Data on ventilation patterns and metabolite excretion rates are currently available only for a limited number of macrofauna species from specific experimental or in-situ conditions. Moreover, there is a complex, non-linear relationship between population density and physiological activity of individual macrofauna [Bridges et al., 1996]. Consequently, a deterministic description of burrow ventilation, metabolite build-up, and resulting temporal dynamics in the burrow water chemistry for a consortium of macrofauna is complicated.

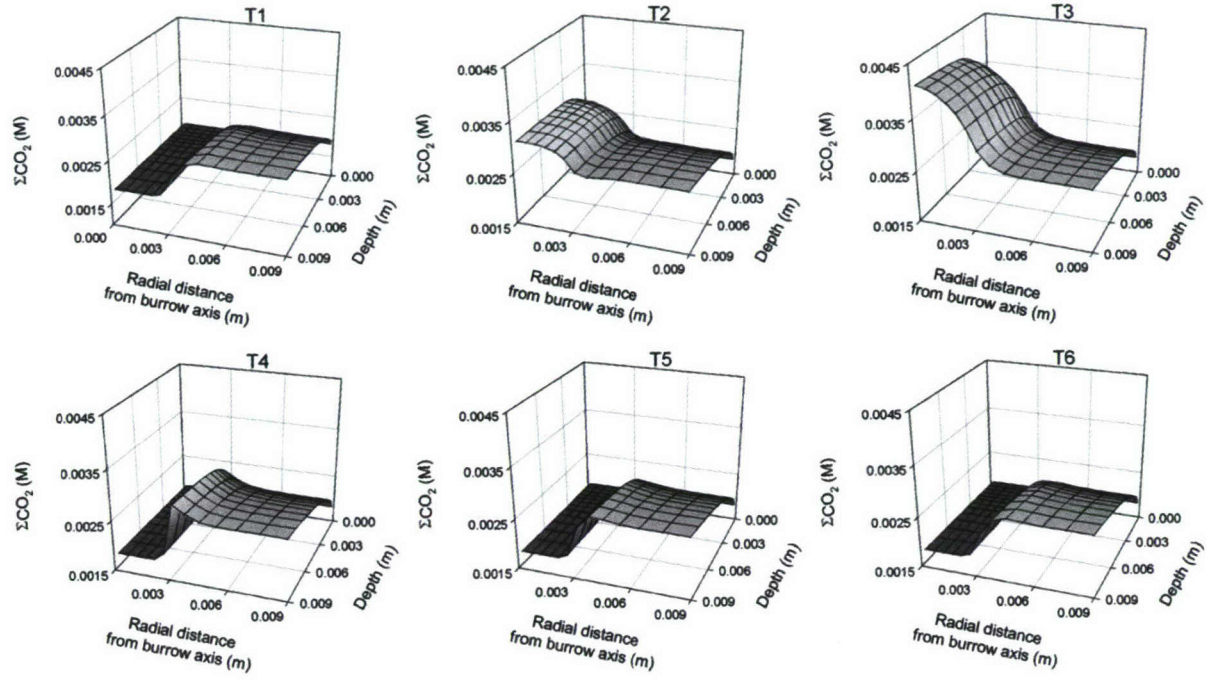

Figure 6. Model-calculated evolution of ΣCO_2 near the WSI and a burrow wall during rest– ventilation cycles of *Nereis virens* (54 min/cycle). At the beginning of the rest cycle (T1 = 0 min), the burrow water ΣCO_2 concentration is identical to that of overlying water and WSI. It becomes enriched during the rest period, as seen at halfway into the rest period (T2 = 20 min) and at its (T3 = 40 min), primarily due to the infauna excretion. Immediately following the rest period, the infauna begins ventilating (T4 = 40 + Δt min), resulting in the maintenance of burrow water ΣCO_2 level as seen halfway into the ventilation period (T5 = 47 min) and at its end (T6 = 54 min).

However, the available burrow ventilation data [Forster and Graf, 1995; Kristensen, 1989; Kristensen, 2001; Riisgård, 1991] can be used as a guide in preparing stochastic descriptions of burrow ventilation, metabolite build-up, and resulting temporal burrow water dynamics. For example, the duration of each ventilation-rest cycle is in the order of minutes to tens of minutes. It may be reasonable to assume that the net rate of metabolite excretion by the consortium of infauna is positively (but perhaps not linearly) related to the total macrofaunal biomass. More data on each individual species of interest in different laboratory or in-situ environments will aide further generalization in determining macrofauna-induced burrow water dynamics.

Biogeochemical Dynamics of Burrow Walls and Their Immediate Vicinities

The above model simulation of the oscillation of redox and major solute chemistry inside of and immediately adjacent to burrows illustrates the dynamic biogeochemical environment of burrow walls and their immediate vicinities. Geochemical oscillations may be restricted to the few millimetres of burrow walls while the porewater chemistry beyond that region may be determined by the time-averaged burrow water composition [e.g., Figure 6]. However, burrow walls are quantitatively significant as they can account for a considerable portion of the available interface between advectively circulated overlying water and sediments in addition to the WSI at the seabed. For example, at a salt marsh bioturbated with *Uca pugnax* in Skidaway Island, over 50% of the interface is accounted for by burrow walls [Furukawa et al., 2004]. Burrows of *Nereis diversicolor* population increase the interface several fold in a shallow mudflat in Limfjorden, Denmark [Nielsen et al., 2004]. While the cylinder approach by Aller [1980] and other simplified geometries may be combined with the boundary conditions of burrow water composition dynamics to describe quantitatively the transport framework of burrowed sediments, they do not offer mechanistic insight into the biogeochemical reaction regimes. Burrow walls have sometimes been assumed to be biogeochemically and structurally identical to WSI (e.g., in terms of labile OC concentrations, OC degradation rate constants, and diffusive tortuosity) in previous modeling studies including the one resulting in Figure 6 [Aller, 1980; Furukawa et al., 2001; Marinelli and Boudreau, 1996]. Meanwhile, other studies have recorded the unique properties of burrows and burrow walls [Aller and Yingst, 1978; Aller et al., 1983].

Consequently, an increasing number of studies are now investigating how properties of burrow walls and their immediate vicinities differ from the conditions found at the WSI, as more advanced tools have become available. For example, the microbial community structures of burrow walls of three marine infaunal species were found to be significantly different from those of the nearby WSI or surrounding anoxic sediments [Noble et al., 2000; Steward et al., 1996]. A study of ghost shrimp burrows, on the other hand, revealed that microbial properties were similar in burrow wall and WSI sediments [Bird et al., 2000]. As microbial community structures are tightly coupled to the biogeochemical properties (e.g., OC degradation reaction rates), the observed differences or similarity in microbial community composition between WSI and burrow walls affect how we can generalize and model the biogeochemical dynamics of burrow walls.

The often unique microbial community composition and associated biogeochemical properties of burrow walls relative to the WSI are the results of: (i) differences in aqueous chemical dynamics (e.g., nearly steady-state chemistry at the WSI in contrast to oscillating chemistry at burrow walls as depicted in Figure 6); (ii) differences in physical and chemical structures (e.g., some species line their burrows with tightly packed particles or organic lining); (iii) potential macrofaunal excretion of uncommon chemicals (e.g., brominated

aromatics [Lovell et al., 1999]); and (iv) short-term stable nature of burrows in contrast to WSI that may experience sudden erosion events. Consequently, the differences between burrow wall and the WSI must be examined at the site- and species-specific basis.

Aller [1983] documented that the diffusive tortuosities of burrow walls constructed by eight infaunal species are greater than that of the WSI owing to infaunal excretion of organic burrow linings or packing of burrow walls by mineral particles. As a result, diffusive exchange of solutes across burrow walls was found to be slower than the diffusive exchange at the WSI by 10–40%. Organic linings produced by many infaunal species are composed of labile OC, resulting in an increased number of microorganisms and enhanced rate of OC remineralization in the immediate vicinity of burrow walls [Kristensen, 2000]. On the other hand, some species line their burrows with inert OC materials that result in decreased microbial activities [Kristensen et al., 1991a]. An experimental study with artificially manipulated burrows showed that the presence of organic linings, as well as the burrow residence time (i.e., time since burrow was created), affect the microbial community structure [Marinelli et al., 2002]. Goni-Urriza et al. [1999] attributed the difference in microbial community structure between bioturbated and control sites to the grain size sorting during macrofaunal sediment ingestion and egestion, while Lucas et al. [2003] showed that the number of microorganisms incorporated into sediment aggregates is decreased after passage through the gut of a deposit feeder. Some species of burrowing macrofauna may excrete bromophenols, a potential biocide that results in markedly distinctive microbial communities in the vicinity of burrow walls compared to the WSI [Steward et al., 1996]. Calculated O_2 consumption rates at the WSI and burrow walls from measured O_2 profiles near a large burrow inhabited by *Uca pugnax* in the salt marsh of Skidaway Island, Georgia, USA, point to a more active aerobic community at WSI than at burrow walls [Table 1]. This may be caused by low and variable O_2 supply to burrow walls as a result of periodic burrow flushing compared with the steady supply of O_2 at WSI, too short burrow residence time for walls to reach biogeochemical steady state, and lack of secreted organic burrow lining by fiddler crabs. Oscillations of other geochemical parameters such as pH at burrow walls may also contribute to differences in microbial communities and activities.

These results reiterate that biogeochemical dynamics of burrow walls is site- and species-specific. No attempt has yet been made to explicitly generalize and/or model

TABLE 1. Oxygen consumption at WSI and along the walls of four *Uca pugnax* burrows at a saltmarsh of Skidaway Island, Georgia, USA, in August 2001. The rates were calculated from measured O_2 microprofiles and for burrows a cylindrical diffusion geometry was presumed (i.e., Figure 3). Clarke-type glass microelectrode was used in conjunction with a micromanipulator at 0.1 mm spatial resolution. The O_2 consumption rate was calculated by solving the ordinary differential equation for steady-state diffusion-reaction by assuming that the burrow walls have achieved geochemical steady state at the time of microprofiling [Cai and Sayles, 1996].

Profile location	O_2 consumption rate (moles L^{-1} s^{-1})
WSI	$1.30 (\pm 0.28) \times 10^{-6}$
Burrow #1	$1.14 (\pm 0.20) \times 10^{-7}$
Burrow #2	$5.36 (\pm 0.45) \times 10^{-7}$
Burrow #3	$2.71 (\pm 0.42) \times 10^{-7}$
Burrow #4	$5.45 (\pm 5.11) \times 10^{-7}$

interactions between different infaunal species, burrow characteristics, and the associated microbial communities. Generalizations are complicated because some interactions enhance the OC remineralization rates (e.g., active aerobic communities; and labile OC burrow lining) whereas others retard the rates (e.g., greater diffusive tortuosity due to grain packing at burrow walls; inert OC burrow lining; redox and pH oscillation of the microbial habitats; and excretion of biocides). Generalizations based on the infaunal population density alone would certainly not work, as various infaunal species are diverse in their burrowing and burrow ventilation habits [Rabouille et al., 2003]. Further understanding of the significance of biogeochemical dynamics in burrow walls for the overall diagenesis may be accomplished through a functional group analysis in which the classification is based on the burrow characteristics, such as the wall materials and burrow ventilation habits [Francois et al., 2002; Pearson, 2001].

Infauna-Induced Particle Displacement

The above arguments have assumed in large part that burrows are physically static structures, and that redox oscillations are controlled by irrigation alone. In reality, however, infauna are constantly burrowing into previously closed sediments for feeding and habitat building, and relict burrows are being infilled by sediment particles. Consequently, new oxic-anoxic interfaces are constantly created and existing interfaces disappear while particles are transported between different redox zones. Thus, infaunal burrowing activities permit sediment particles to experience temporal redox oscillations, as well as oscillations of related geochemical parameters. The redox oscillation scenarios are potentially significant in determining the courses of sedimentary chemical mass transfer, for example, because elevated OC remineralization rates have been reported in redox-oscillating experiments [Aller, 1994; Hulthe et al., 1998].

In the past, laterally and temporally averaged particle displacement has been estimated from the vertical profiles of radionuclides and successfully described using diffusive expressions assuming vertical geometry [Demaster and Cochran, 1982; Rice, 1986]. Computer-assisted optical tracer techniques have enabled the description of short-term particle displacement in 1D geometry [Gilbert et al., 2003b]. However, such averaged strategies do not allow for a complete description of redox/geochemical oscillations. For example, a sediment particle experiencing oscillating redox state may in the averaged approach be considered at a constant state that is somewhere between the oxic and reduced endmember.

Aller [1984] suggested that redox-oscillating environments can be regarded as distinct functional states. Modeling such conditions can provide reaction and transport parameters that are distinctively different from those obtained for environments at steady state or unidirectionally changing redox regimes. For example, redox oscillations promote the formation of poorly-crystalline Fe(III) minerals such as ferrihydrite, that are more rapidly utilized as terminal electron acceptors (TEA) than crystalline Fe(III) [Furukawa et al., 2004; Jensen et al., 2003]. Furthermore, the rate of aerobic degradation is significantly higher for OC kept under an anaerobic conditions until recently, compared to OC that has been under a continuously oxic conditions [Hulthe et al., 1998].

These examples justify the use of separate reaction rate parameters for redox oscillating environments. However, most direct measurements of microbial OC degradation and microbial TEA reduction rates under variable redox conditions are conducted at limited temporal scales (e.g., simple differences between oxic and anoxic degradation) [Jørgensen and Bak, 1991; Kristensen et al., 1995; Sun et al., 1993], which cannot be used to quantify the degradation in natural redox oscillating environments. There is instead need for experiments conducted in

systems with redox cycles that simulate burrow environments. In order to apply results of such redox oscillation experiments in actual bioturbated sediments, we must have *a priori* understanding of the nature of redox oscillation parameters (in terms of both magnitude and cycle length) for typical sedimentary particles that reside in the bioturbated zones.

Measurements of OC degradation and other biogeochemical reaction in explicitly manipulated redox regimes have only been conducted in few recent studies. These have shown that degradation rates of certain lipid compounds are positive (but not necessarily a linear) functions of the duration of oxic periods when the oxic/anoxic alternation occurs at two- to eight-day cycles [Figure 7] [Sun et al., 2002a; Sun et al., 2002b]. A similar result was obtained using different sediment substrates under a similar oxic/anoxic alternation pattern [Caradec et al., 2004]. A naturally occurring consortium of sedimentary OC compounds, on the other hand, were found to degrade at approximately the same rate in a completely oxic experimental assay and in an oscillating assay which experienced oxic conditions 20% of the time [Aller, 1994]. In addition, oxic degradation of sedimentary OC that had been kept anoxic for about 14 years was more extensive than oxic degradation of freshly deposited sedimentary OC, implying that prolonged anoxic conditions may help the transformation of inert OC into a form that is readily oxidized under oxic conditions [Hulthe et al., 1998].

These contrasting experimental results suggest that the correlation may depend not only on the types of OC species and the pattern of oxic/anoxic alternations, but also on differences in microbial community structure (e.g., net abundance, relative abundance between Fe(III) reducing bacteria and sulfate reducing bacteria) that develop under different redox regimes. The appropriate reaction and transport parameters can only be derived by an array of experimental studies with a range of different OC compounds typically for sedimentary

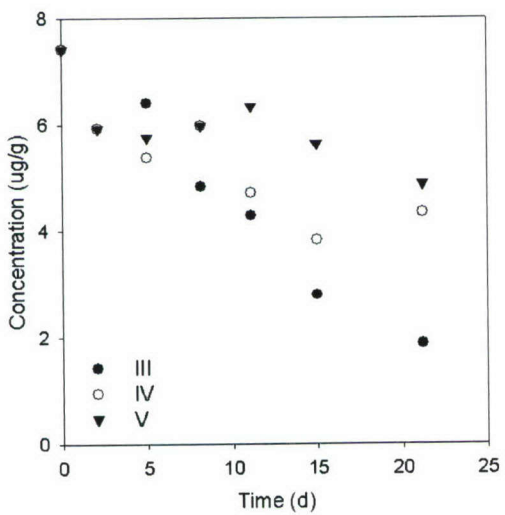

Figure 7. Degradation of ^{13}C-labeled alkene in laboratory microcosms. Sample III experienced alternating oxic and anoxic periods, each lasting 24 h. Sample IV was subject to cycles of redox oscillation, each cycle consisting of 24 h of oxic period followed by 72 h of anoxic period. Sample V underwent oscillation cycles with 24 h of oxic period followed by 168 h of anoxic period. From Sun et al. [2002a].

environments and under different redox oscillation regimes. Although limited in numbers, the existing studies of OC degradation under deliberately manipulated redox conditions [Caradec et al., 2004; Sun et al., 2002a; Sun et al., 2002b; Sun et al., 1993] provide guides to further experimental studies. It is important to test a range of microbial community structures in this context to provide mechanistic rationales for correlations between oxygen exposure time, oscillation patterns, and reaction rates.

However, effects of redox oscillation on OC degradation rates can only be evaluated properly when we have knowledge on the redox oscillation patterns that actually occur in sediments. Redox conditions experienced by any particle are directly related to the movement of that particle across redox zones. A few studies have aimed to quantify particle movement using non-diffusive and non-local model frameworks such as those summarized by Meysman et al. [2003]. For example, a recent study used optically tagged particle tracers (i.e., luminophores [Gerino, 1990]) and traditional coring methods to quantify bioturbation in the Vece Lagoon, and described it with a model that has both diffusive and non-local terms [Mugnai et al., 2003]. Another study combined luminophores with in situ imaging of 2D sediment profiles (i.e., SPI Camera [Rhoads and Germano, 1982]) to obtain high- frequency time-lapse data on macrofaunal particle transport, which were then described using a non-local, non-diffusive model framework [Solan et al., 2004]. Results of these and future similar studies will ultimately enable us to reliably estimate the range of redox oscillation patterns encountered by sediment particles within various environments. Combined with the understanding of relationships between redox oscillation patterns and OC degradation rates, properly described particle displacement regimes will become an important part of a comprehensive description of sediment biogeochemistry.

Direct Infaunal Metabolization of Organic Carbon

Investigations of sedimentary OC diagenesis have for many years focused on microbially mediated remineralization of OC. These processes are considered homogeneous in the temporal and spatial scales applicable to many of the approaches that studies of early diagenesis have been intended for, such as the quantitative determination of OC preservation potential, contaminant bioavailability and cycling of carbon and nutrients. In the context of microbial diagenesis, the effects of infauna have mostly been discussed in terms of their influence on the transport regimes and microbial activity. However, macrofauna also participate directly in the respiration of a TEA (i.e., oxygen), consumption (i.e., degradation) of OC, and production of metabolites such as CO_2 and NH_4^+, in significant quantities at the temporal and spatial scales applicable to our interests. A growing number of studies in recent years have documented the quantitative significance of the OC metabolism by infauna themselves.

Studies using pulse inputs of radiolabeled OC have revealed a spatially and temporally heterogeneous nature of infaunal OC remineralization in various environments. Infaunal populations from the continental slope off North Carolina ingested a large fraction of a pulse OC input within few days whereas the remainder was subducted down to > 10 cm sediment depth in association with the burrow excavation activities [Blair et al., 1996; Levin et al., 1997]. Approximately 17% of a pulse OC input to a continental slope site off the west coast of Norway was processed (i.e., fully or partially remineralized) by macrofauna [Witte et al., 2003a; Witte et al., 2003b]. The concurrent oxygen consumption was significantly increased due to macrofaunal respiration, even though macrofauna were responsible for less than 5% of the total sedimentary biomass. In the oxygenated part of

the northwestern Black Sea, macrofauna were responsible for up to 70% of the OC degradation [Wenzhofer et al., 2002]. Thus, seabed fluxes of dissolved O_2 may be elevated in the presence of bioturbating organisms not only because of the increased oxic – anoxic interface area as demonstrated in Figure 1, but also because of the O_2 respiration by macrofauna [Rabouille et al., 2003].

The contribution of macrofaunal metabolism to overall OC diagenesis may therefore be generalized using the macrofaunal biomass as the control variable. For example, there is a positive correlation between the biomass of bivalves and O_2 demand on the bottom of the Black Sea, although these animals do not adapt to the varying dissolved O_2 concentration. Accordingly, the relationship is not simple, as the physiological response of macrofauna to the input of OC is non-linear. Some species partially remineralize OC boosting microbial activities [Witte et al., 2003b], whereas others cause subduction of fresh OC deep into their burrows where OC may be isolated from the abundant aerobes of the WSI [Levin et al., 1997]. Moreover, feeding strategies may affect the magnitude of macrofaunal metabolism as some species (e.g., suspension feeders) may react to the temporal change in OC fluxes whereas others (e.g., deep-deposit feeders) may not. The generalization of macrofaunal metabolism would benefit from a functional group analysis that is based on the feeding patterns and the chemical constituents of ejected, partially remineralized OC.

Summary and Conclusions

The major challenge facing the comprehensive, generalized understanding of biogeochemical consequences of infauna activities is their site- and species-specific nature. The most significant impacts of infaunal activities on sediment biogeochemistry are: (1) creation of spatially complex geometries that influence the diffusive transport of redox species; (2) creation of temporally dynamic redox and geochemical regime that control the microbial activities through burrow excavation, periodic ventilation of burrows, and particle transport between different redox conditions; and (3) infaunal participation in the OC remineralization causing temporally and spatially heterogeneous respiration of a TEA (i.e., O_2) and metabolization of OC. Although these infaunal involvements in general have positive influences on the rates and magnitudes of OC degradation, there are exceptions due to e.g. inert burrow linings and biotoxic metabolites excreted by some infauna. Moreover, the quantitative effect of infaunal activities on net OC degradation depends on the external forcings such as the dynamics of labile OC flux and sediment dynamics.

The laterally heterogeneous solute transport geometry due to infaunal burrows has been successfully expressed using the burrow surface area per unit volume of sediments. However, such expression requires direct observations of the burrow structures that are time consuming. More data on burrowing schemes for infauna commonly found in the environments of our interests will allow future stochastic descriptions of the burrow surface area per unit volume.

The physical dynamics of burrow water has been directly measured for a limited number of infaunal species. The biogeochemical dynamics, which are more difficult to measure, can be estimated through model calculations when physical dynamics data are available. More data on burrow ventilation and metabolite production schemes for common infauna would further assist us in determining the quantitative significance of periodic burrow ventilation and metabolite build-up in overall diagenesis.

Currently very little is known about the biogeochemical properties of burrow walls. The current data are limited to the stable burrows of a small number of infaunal species in specific environments. Microbial and geochemical analyses specifically for burrow walls

are labour intensive and are overwhelming to do for all possible species. Current efforts on the biogeochemical descriptions of burrow walls should be combined with a functional group classification in order to achieve more generalized understanding of the burrow wall biogeochemistry.

Infauna-induced particle displacement has been successfully studied for many years using radionuclide tracers. New tracers (e.g., Luminophores) together with the computer-assisted tracer analysis would add to the current suite of tools by providing the means to determine short-term particle displacement patterns which will aide comprehensive descriptions of the redox oscillations experienced by sediment particles. The forthcoming experimental knowledge of redox oscillations due to particle displacement needs to be coupled to the increasing data on the effect of redox oscillation on biogeochemical mass transfer. Such data may be accumulated through rate measurements in deliberately redox-manipulated microcosms.

The study of direct infaunal effects on early diagenesis has just started. Techniques involving isotope-labeled OC have been a great tool in advancing our understanding in this area. More data are needed, and perhaps the use of molecular techniques would help us understand the effects of infaunal metabolism in environments where the introduction of deliberate tracers is not feasible.

Although the above summary calls for more experimental data, it is essential that the scientific community continues its modeling efforts as well. Modeling can fill the gaps where direct experimental data are lacking by using stochastic descriptions, parameter adjustments, or inverse approaches. A failure to describe the observed phenomena by a model after simple parameter adjustments may indicate lack of understanding associated with the parameters, and thus can direct the course of further experimental studies. Moreover, a complete, quantitative description of complex, interdependent processes such as those described here can be accomplished only through a comprehensive, computational model framework that combines the quantitative description of each process simultaneously.

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